OSTEOLOGY AND RELATIONSHIPS OF THE PROCHILODONTIDAE, A SOUTH AMERICAN FAMILY OF CHARACOID FISHES

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ABSTRACT. Little studied and poorly known, Prochilodontidae are among the most important of the inland food fishes in South America. A brief review of their biology is presented in the Introduction, followed by an account of their osteology. Observations are also given on the soft anatomy of the trophic structures. Prochilodontidae usually have been regarded as close relatives of the Curimatidae, but there are no shared specializations in support of such relationship (with the possible exception of paired epibranchial pouches). Rather, highly specialized features of the jaw suspension indicate they are closely related to Anostomidae and Chilodontidae. They have a number of unique specializations, especially of the trophic structures, which distinguish them from other characoids and support their taxonomic rank as a separate family.

INTRODUCTION

The thirty or so species of Prochilodontidae, all medium or large sized, comprise some of the most important fishes consumed in Ecuador, Colombia, Venezuela, the Guianas, Brazil, Perú, Bolivia and Argentina. Members of the family can be recognized at a glance by their characteristic appearance (Fig. 1). Superficially resembling some of the larger African and Asian fishes of the cyprinoid genus *Labeo*, they are iliophytophagous, ingesting mud, diatoms, periphyton and organic detritus. The enlarged, fleshy lips bear exceedingly numerous minute teeth and can be everted into a broad rasping (and suctorial?) disc.

There are only three genera of Prochilodontidae: *Ichthyoelephas, Semaprochilodus,* and *Prochilodus* (Mago Leccia, 1972). *Ichthyoelephas,* with only two species, has a very restricted range: one species in the Guayas basin on the Pacific coast of Ecuador, the other species in Pacific and Atlantic coastal river systems of Colombia, including the Río Magdalena. *Semaprochilodus,* with four species, has its range centered in the Amazon and Orinoco basins. It probably does not occur south of the Amazon. It should be noted that the type species of *Semaprochilodus, S. squamilentus* Fowler (1941: 170–174, fig. 83) is based on specimens purportedly collected from the Rio Parnaíba at Therezina in northeastern Brazil. This report, like that of *Boulengerella cuvieri* from the same locality (*ibid.,* p. 194, fig. 103), is almost certainly based on specimens having erroneous locality labels. Long-term collecting efforts in the Rio Parnaíba subsequently conducted by Sr. R. Adhemar Braga (Serviço de Piscicultura, Departamento Nacional das Obras Contra as Sêcas) at Therezina and other localities have failed to produce a specimen of either genus. Sr. Braga and I suspect that the *Semaprochilodus* (and *Boulengerella*) in question originated from the market in Belem-do-Pará and were inadvertently included with lots collected at Therezina. In all probability *S. squamilentus* is a junior syno-

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nym of one of the well-known Amazonian species. *Prochilodus*, with some 24 species, is very widely distributed. It occurs in the Magdalena basin, in the Guianas, throughout the Amazon, Orinoco, and Plate basins, and in most of the larger separate river systems of Brazil, including the Rio São Francisco.

It is well known that *Prochilodus* and *Semaprochilodus* undertake extensive upstream spawning migrations, after the onset or at the height of the rainy season (Ihering and Azevedo, 1934); Godoy, 1959, 1967; Schaller, 1968; Mago Leccia, 1972). The tremendous schools of *Prochilodus platensis* in the Río de la Plata (Ringuelet *et al.,* 1967: 206–7) are perhaps larger than the schools of any other species of freshwater fish in South America. Several species are noted as accumulating considerable fat deposits before the reproductive season, presumably as reserves for the spawning migration. Prochilodontidae are also known for the extremely large number of eggs they produce. The two ovaries of a *Prochilodus argenteus* of 640 mm in total length contained over 600,000 eggs (Fontenele, 1953).

Fishermen on the Amazon say they can distinguish different species of spawning Prochilodontidae by the sounds they make (personal communication from Prof. George S. Myers). During the spawning migration, males of *Prochilodus argenteus* emit a very loud and characteristic sound ("ronco") audible above the water surface. The sounds increase in intensity as spawning occurs (Fontenele, 1953). Schaller (1968) published a spectrogram of the sound made by a school of *Semaprochilodus.* They made a noise like that of a motorcycle. Actual spawning may occur in shallow water almost anywhere along the course of large rivers, sometimes below obstacles such as waterfalls. There are several reports that Prochilodontidae spawn at night: Ihering and Azevedo (1934) for *P. argenteus;* Godoy (1959) for *P. scrofa;* and Schaller (1968) for *S. insignis.* After spawn-

ing, the fishes form large schools that move downstream back to the feeding grounds.

The mechanism of sound production in the spawning males is not well understood. Fontenele (1953) reported vibratory movements of the opercular covers as the sounds were emitted, but such movements are possibly a secondary effect. Schaller (1968) suggested that sound is produced by vibration of the circular opening between the anterior and posterior chambers of the swim bladder, when air is forced from the anterior chamber into the posterior chamber by contractions of the epaxial muscles. Whether males of *Ichthyoelephas* produce sounds comparable to those of *Prochilodus* and *Semaprochilodus* is unrecorded. Comparable sounds have not been reported in any other family of characoids.

Techniques inducing *Prochilodus* to spawn in captivity, by means of injecting pituitary extracts, and for rearing the eggs and young until they are old enough for stocking, were developed by Brazilian fishery biologists (Fontenele *et al.,* 1946; Fontenele, 1953). Hatchery-produced *Prochilodus* have been stocked in açudes or reservoirs in northeastern and southeastern Brazil for more than 20 years. *Ichthyoelephas humeralis* and *I. longirostris* are among the most promising indigenous species in Ecuador and Colombia for stocking and fish culture.

A key to the genera of Prochilodontidae is given by Mago Leccia (1972) in his revision of the species in Venezuela. The family should be revised on a continentwide basis. Citations of virtually all important systematic references can be found by consulting Eigenmann, 1912, 1922; Fowler, 1948-1954; Ringuelet *et al.,* 1967; and Mago Leccia, 1972.

The purpose of the present paper is to provide morphological and osteological information on Prochilodontidae as a basis for studies of their trophic habits, functional anatomy, and phyletic relationships to other characoids. Previous osteological
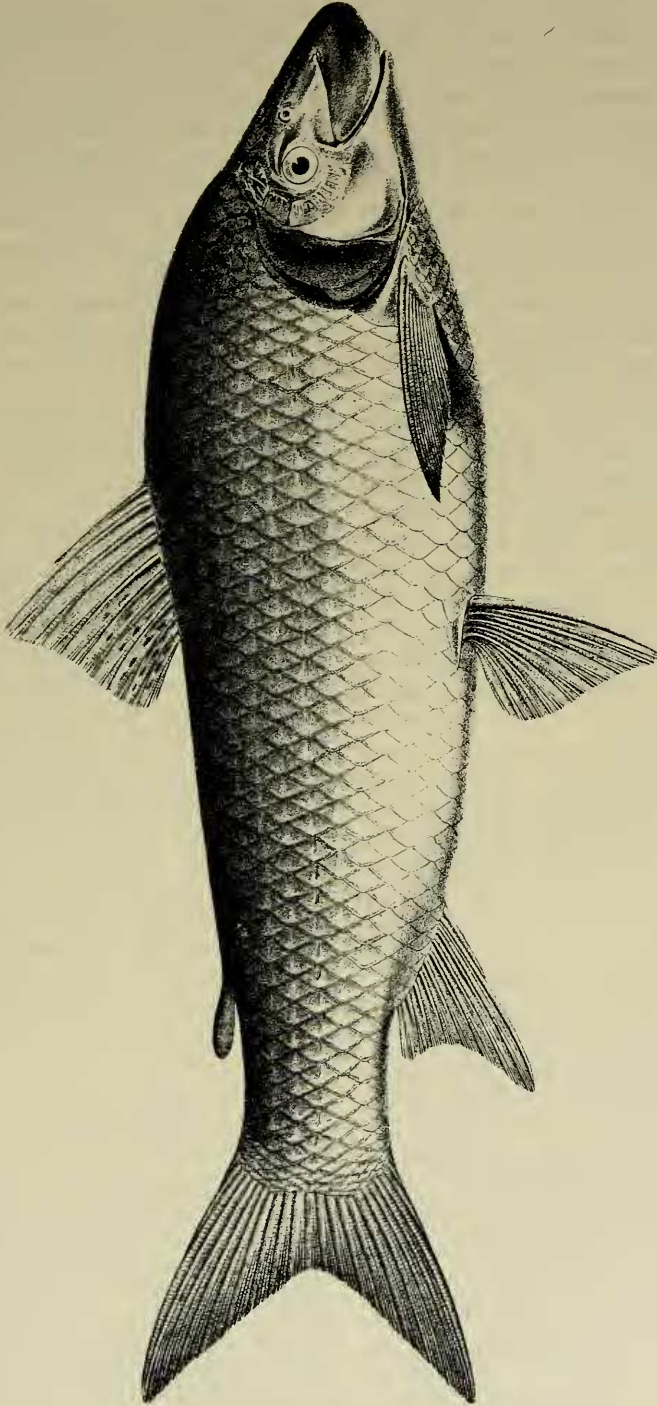
Figure 1. *Ichthyoelephas longirostris*, from the Río Cauca, Colombia (from Steindachner, 1880).

work on Prochilodontidae is limited to brief observations by Regan (1911) and to figures illustrating superficial differences in the crania of *Ichthyoelephas* and *Prochilodus* (Miles, 1943: 46). Schaller (1968) gave a brief description and figures of the swim bladder of *S. insignis*. I am unable to provide any further information concerning the mechanism of sound production. The most important conclusions reached herein concern the relationships and systematic status of Prochilodontidae. There is little in the way of shared specializations to indicate relationship with Curimatidae. The structure of the suspensorium of the jaws shows highly specialized conditions found elsewhere only in Anostomidae and Chilodontidae, and other osteological evidence tends to support the idea of relationship between Prochilodontidae and Anostomidae. The highly specialized dentition and soft anatomical features of both jaws and gill arches provide diagnostic features for the Prochilodontidae and justify its familial rank.

ACKNOWLEDGMENT

OBSERVATIONS

Study material. The osteological observations described below are based on alizarin preparations of the following specimens: *Ichthyoelephas humeralis* (Gunther), MCZ 48723, two specimens, 97.2 and 102.4 mm in standard length; Río Vinces at Vinces, Guayas basin, Ecuador; T. Roberts, R. Gilbert, F. Silva M., 5 November, 1971. *Prochilodus vimboides* Kner, MCZ 20169, two specimens, 94.8 and 103.0 mm in standard length; Rio Paraíba, southeastern Brazil; Hassler Expedition, 1872. *Semaprochilodus insignis* (Schomburgk), MCZ 20129, three specimens, 95.3, 96.7, and 106.7 mm in standard length; lower Amazon River at Villa Bella, Brazil; Thayer Expedition, 1866.

The figures of prochilodontid osteology are based on *Ichthyoelephas humeralis* (hereafter referred to as *Ichthyoelephas*). *Prochilodus vimboides* and *Semaprochilodus insignis* (hereafter referred to as *Prochilodus* and *Semaprochilodus*) were thoroughly dissected and directly compared with *Ichthyoelephas*. In most respects the osteology of the three genera is extremely similar, but there are some noteworthy differences in the suspensorium of the jaws. The soft anatomy of the trophic structures is also closely similar in the three genera.

Cranium (Figures 2–5). Ethmoid bone relatively large and broad, especially in *Ichthyoelephas*, with a thin, ventrally directed median lamina. Ethmoid spine broadly rounded. Shape of ethmoid somewhat similar to that in anostomids such as *Leporinus* and *Schizodon*. Ethmoid with a short posterolateral process contacting a process from lateral ethmoid.

Vomer expanded anteriorly into a rounded plate, from which a dorsally directed median lamina projects. Head of vomer with a prominent pair of synchondral joint surfaces for ethmoid. Unlike Curimatidae, no substantial block of cartilage between vomer and ethmoid.

Lateral ethmoids large, with slender anterior processes contacting ethmoid (an unusual condition in characoids) and posterior processes contacting orbitosphenoid. In some specimens orbital blade or lamina of lateral ethmoids highly fenestrated (*cf.* Fig. 4).

Frontals broad, deeply notched posteriorly for dilator fossae. Dilator fossae not extending onto dorsal surface of frontals. Notch in frontals covered by closely adherent sixth infraorbital or dermosphenotic. Frontoparietal fontanel narrow, open for its entire length in juvenile *Prochilodus* and *Semaprochilodus*. In juvenile *Ichthyoelephas* only frontal portion of fontanel open, a relatively rare condition in characoids (occurs in some specimens of *Leporinus*). In large adults of Prochilodontidae frontoparietal fontanel some-

times entirely closed. Frontals bear extremely branched laterosensory canals.

Rhinosphenoid absent. Orbitosphenoid receiving well-developed processes from lateral ethmoids. Orbitosphenoid with ventrally directed process joined to parasphenoid in *Semaprochilodus* and *Prochilodus*. Similar process absent in *Ichthyoelephas*. Parasphenoid anteriorly and posteriorly with a well-developed ventromedian lamina. Parasphenoid terminating in a slight notch posteriorly, not deeply cleft.

Posttemporal fossae each with two well-developed openings, as in most (all?) Characidae and in Anostomidae. Parodontidae, Hemiodontidae, and (all?) Curimatidae have three openings into each posttemporal fossa. Subtemporal fossae well developed. Intercalar bone bridging a sizeable recess in posteromedial corner of subtemporal fossa. Prootic, pterotic and sphenotic with well-developed facets for hyomandibular joint. Lagenar capsules moderately large. Curimatidae with exceptionally large lagenar capsules. Pterotic with a well-developed posteriorly directed spine. Epiotic spineless. Supraoccipital spine enlarged, relatively deep and moderately elongate but narrow based.

Otoliths (Figure 6). Otoliths superficially similar to those of many other characoids, including *Brycon* (*cf.* Weitzman, 1962, fig. 7 of *Brycon meeki* otoliths).

Jaws; dentition (Figures 7–11). Greatly enlarged lips and gums of Prochilodontidae form a large, round, suckerlike disc when mouth fully opened. Entire rim of disc provided with minute labial papillae (not figured) and minute spatulate or ciliate teeth. In a 97.2-mm *Ichthyoelephas* there are around 600 functional teeth on periphery of oral disc. Teeth comparably numerous in *Prochilodus* and *Semaprochilodus*. Number of teeth on rim of oral disc increases (linearly?) with size of individual. In addition to functional teeth on rim of oral disc, there are two inner V-shaped rows of morphologically similar but slightly enlarged teeth, one row in upper lip and one row in lower lip. Within fleshy mouthparts lie row upon row of preformed replacement teeth. *Semaprochilodus* of 95.3 to 106.7 mm with only three to five rows of replacement teeth for functional row on rim of oral disc; *Prochilodus* of 94.8 to 103.0 mm with six to eight rows of replacement teeth; and *Ichthyoelephas* (*I. humeralis*) of 97.2 to 102.4 mm with ten to twelve rows of replacement teeth. Number of rows of replacement teeth presumably increases with increasing size of individual. *Ichthyoelephas longirostris*, with largest soft mouthparts of any Prochilodontidae, presumably also with largest number of replacement tooth rows. Perhaps closely packed rows of replacement teeth stiffen oral disc or perform some other mechanical function. To judge from the number of functional teeth and the number of rows of replacement teeth, more tooth replacement occurs in Prochilodontidae than in any other characoids.

Functional teeth movable, because they attach only to soft tissues of lips and gums. All teeth closely adjacent to each other, with crown of each tooth curved so that it overlaps tooth posterior to it (Fig. 7), thus transferring pressure on any one tooth to several more teeth anteriorly. Mago Leccia (1972) pointed out morphological differences between the teeth of *Ichthyoelephas*, *Semaprochilodus* and *Prochilodus* (Fig. 8). Range of tooth shapes greater in *Prochilodus* than in other two genera (personal observation).

Premaxillary movably articulated with ethmoid but not truly protractile. Curvature of premaxillary and maxillary provides greater area for attachment of lips and gums. Maxillary with well-developed anterior process for attachment of tendon from adductor mandibulae, and posterior process for maxillomandibular ligament. Maxillary (but not premaxillary) with several large foramina.

Lower jaw (Fig. 9) extremely modified,

its morphology distinct from that of other characoids. Jaw heavy and compact in construction, and foreshortened. Replacement tooth trench (typically present in lower jaw of characoids but absent in upper jaw) very deep and broadly open, with a single large foramen in its posterior wall. No fenestra at point where upper limb of articular passes externally to dentary. Such a fenestra usually (always?) present and well developed in Curimatidae and in characoids with normally elongate jaws. Dentary with a medial shelf bearing a stubby, dorsally directed flange partially overlying coronomeckelian bone and entirely overlying anteromedial process of articular bone. Proximal part of angular bone snugly tucked into a pocket in ventral margin of articular bone. In this feature and in their compaction and general morphology, prochilodontid lower jaws resemble those of Anostomidae more than any other characoids (*cf*. Figs. 12–13 of *Schizodon*). In contrast, jaws of hemiodontids and curimatids relatively elongate and of generalized characoid morphology, with angular bone exposed, a fenestra between articular and dentary, and anteromedial process of articular lying exposed on a medial surface of dentary (*cf*. Fig. 14 of *Acuticurimata macrops*).

Suspensorium and opercle (Figures 10–11). Suspensory apparatus of jaws composed of quadrate, symplectic, preopercular, palatine, ectopterygoid, mesopterygoid, metapterygoid, and hyomandibular. In addition three autogenous canal bones associated with preopercle—a suprapreopercle and two subpreopercles. Relationships of quadrate, preopercular, subpreopercles and interopercle highly specialized in prochilodontids, providing information of phyletic significance: similar specializations otherwise occur only in Anostomidae and Chilodontidae. In Prochilodontids quadrate with a broad, elongate, lateral flange or trough forming a shelf underlying the massive adductor mandibulae muscles. Quadrate also with a posteriorly directed process extending medially alongside anterior end

of preopercle. Anterior end of preopercle extends only for a short distance in between this medial quadrate process and lateral flange or trough of quadrate and is thus unusually distant from quadratomandibular joint. Interopercle, which in characoids usually extends anteriorly to near quadratomandibular joint, extends only as far forward as preopercle. In consequence, preopercular segment of preoperculomandibular sensory canal passes anteriorly through two separate subpreopercular canal bones before reaching mandible. All of these highly specialized features also occur in Anostomidae such as *Leporinus* and *Schizodon* (*cf*. Figs. 12–13 of *Schizodon*), in which quadrate bone and its lateral trough or flange are even more elongate than in Prochilodontidae. In contrast, relationships of quadrate, interopercle and preopercle in Curimatidae are relatively generalized (*cf*. Fig. 14 of *Acuticurimata macrops*).

As in Parodontidae, Hemiodontidae, and Anostomidae (but not in Curimatidae), ectopterygoid movably articulated to quadrate. Mesopterygoid and metapterygoid, however, firmly united. Union between meso- and metapterygoids in Parodontidae, Hemiodontidae, and Anostomidae loose. Metapterygoid-quadrate foramen distinctive in that its dorsal border (formed by metapterygoid) is straight or slightly convex, rather than deeply indented as in typical Characidae, Hemiodontidae, Curimatidae (Figs. 14–15), and Anostomidae (Figs. 12–13). In *Ichthyoelephas* mesopterygoid relatively small, falling far short of palatine; in *Prochilodus* mesopterygoid larger; and in *Semaprochilodus* much larger, almost reaching palatine. At its movable articulation with quadrate, ectopterygoid forked or notched ventrally, much more so in *Prochilodus* and *Semaprochilodus* than in *Ichthyoelephas*. Symplectic more elongate and more loosely attached to quadrate in *Prochilodus* and *Semaprochilodus* than in *Ichthyoelephas*. Metapterygoid loosely bound to hyomandibular in *Prochilodus* and *Semaprochilodus*, less so in *Ichthyoelephas*.

All prochilodontids with a preopercle, interopercle, subopercle and opercle. Lateral surface of opercle smooth, without strong flange just above hyomandibulo-opercular joint, characteristic of Curimatidae (*cf.* Fig. 16 of *Acuticurimata macrops*). This flange readily detectable in specimens preserved in alcohol, and occurs in many (all?) curimatids, including "*Pseudocurimata*" *ocellata* (Eigenmann and Eigenmann, 1889), which superficially resembles *Hemiodus* very strongly. (Opercular flange absent in *Anodus;* my researches, as yet unpublished, strongly indicate that *Anodus,* despite its toothless jaws, belongs in the family Hemiodontidae rather than in Curimatidae.)

Nasal, antorbital, and circumorbital bones (Figure 17). Circumorbital series complete with a supraorbital, antorbital, and six infraorbitals. Infraorbitals and nasal with both laminar and tubular components. Shape of antorbital and of first infraorbital (lacrimal), and relation of first and second infraorbitals to each other rather similar in prochilodontids and anostomids (*cf.* Fig. 18 of *Schizodon*), although anostomid second infraorbital lacks anteroventrally directed flange characteristic of Prochilodontidae. First infraorbital greatly enlarged. Supraorbital lacking slender ventrally directed process contacting antorbital characteristic of many Curimatidae (*cf.* Fig. 15 of *Acuticurimata macrops*).

Hyoid bar and branchial arches (Figures 19–23). Hyoid bar (Fig. 19) with four greatly expanded branchiostegal rays, three on ceratohyal and one on epihyal. Basihyal moderately expanded anteriorly inside tongue. Interhyal large, its lower end forming a V-shaped joint saddling dorsal surface of epihyal (apparently a unique specialization). Dorsal and ventral hypohyals fused or partially fused and difficult to distinguish.

Soft anatomy of prochilodontid branchial arches (Fig. 20) distinctive and highly specialized. Gill rakers of first four arches stubby and embedded in thick, tough epithelium. First arch bears about four rakers on its upper limb and ten to twelve rakers on its lower limb. Ceratobranchial bones of fifth arch covered by a highly papillose epithelium, with fine papillae arranged in numerous rows perpendicular to main axis of body. This papillose epithelium continues uninterrupted into dorsally situated pair of epibranchial sacs or pouches lying immediately posterior to fourth (last) pair of epibranchial bones. Fourth epibranchial (Figs. 21–22) with a large, dorsally directed lamina. Ventrally it has a well-developed tooth plate bearing two or three dozen minute conical teeth with greatly swollen round bases. No other teeth on prochilodontid branchial arches. Tooth plate articulated to fourth epibranchial bone by a moveable (synovial?) joint (Fig. 22).

Anostomidae bear opposable tricuspid teeth on third and fourth epibranchial and fifth ceratobranchial toothplates, as do Chilodontidae. Prochilodontid epibranchial teeth greatly reduced, apart from their swollen bases, no direct evidence found to indicate derivation of these teeth from tricuspid teeth. In Curimatidae third and fourth epibranchial and fifth ceratobranchial toothplates bear numerous conical teeth (without swollen bases).

Ichthyoelephas with first pair of suspensory pharyngeal bones or infrapharyngobranchials apparently absent. These bones definitely present in *Semaprochilodus* and *Prochilodus.* These first elements easily lost or overlooked, being smaller and more dorsal in position than second through fourth infrapharyngobranchials.

Pectoral and pelvic girdles (Figures 24–25). Prochilodontid pectoral and pelvic girdles of generalized characoid morphology apparently lacking in features of phyletic significance at generic or family levels. Position of forked posttemporal bone in relation to occiput as shown in Figure 5. Pectoral girdle complete, with posttemporal, supracleithrum, cleithrum, scapular, mesocoracoid, coracoid, four proximal radials and three postcleithra.

Third postcleithrum with proximal part expanded, distal part slender.

Pelvic bone with well-developed, elongate ischiac process. Innermost pelvic radial greatly enlarged, comma-shaped, as in many other characoids (cf. Roberts, 1971, fig. 14 of hemiodontid *Micromischodus sugillatus*). Pelvic fin usually with nine rays, although several specimens examined with pelvic fin of one side nine-rayed and pelvic fin of other side ten-rayed.

Weberian   apparatus   (Figure   26). Weberian apparatus of generalized characoid construction, apparently without phyletically significant features at generic or family levels. Comparisons closer than are now possible of Weberian apparatus among more characoid groups may prove informative.

Vertebral counts.   Total vertebral counts in two specimens of *Ichthyoelephas,* 34 and 35; in two *Prochilodus,* 37 and 38; and in three *Semaprochilodus,* 40 and 41 (in two specimens). Abdominal plus caudal vertebral counts in the same specimens are: *Ichthyoelephas,* 23 + 11 and 24 + 11; *Prochilodus,* 26 + 11 and 25 + 13; and *Semaprochilodus,* 26 + 14 and 27 + 14 (in two specimens).

Supraneurals (Figure 27). Supraneurals greatly expanded, four in *Prochilodus* and *Ichthyoelephas,* five in *Semaprochilodus.*

Caudal skeleton (Figure 28). Nomenclature of caudal skeleton followed here is that presented by Monod (1969). Prochilodontid caudal skeleton identical to the generalized or typical caudal skeleton pattern shared by diverse and unrelated characoids, including Curimatidae, Anostomidae, Parodontidae,   and   characids   such   as *Chalceus, Alestes,* and *Brycon* (cf. Weitzman, 1962), fig. 15 of *B. meeki*). Parhypural and six separate hypurals present. Parhypural without a distinct hypurapophysis. No secondary hypurapophysis on first hypural. Parhypural bears a moderately to strongly developed ridge for much or all of its length; this ridge is a continuation of side of hemal arch onto laminar portion of parhypural. Second hypural fused to complex hypural centrum. Two pairs of uroneurals and three epurals present. In common with all characoids, Prochilodontidae have 10 + 9 principal caudal rays.

Caudal skeleton of Hemiodontidae (including *Anodus*) differs significantly from above pattern in having first and second hypurals fused to each other and in having second hypural entirely separated from complex hypural centrum (cf. Roberts, 1971, fig. 15 of *Micromischodus sugillatus*), as verified in all genera of Hemiodontidae, except *Atomaster* (unavailable for study).

DIAGNOSTIC FEATURES OF THE FAMILY PROCHILODONTIDAE

The most distinctive features of Prochilodontidae described above are those having to do with the dentition, both oral and branchial, and with the anatomy of the trophic structures. The dentition is highly specialized and quite unlike that of other characoids. While Curimatidae have highly papillose branchial epithelium and paired epibranchial pouches, the distribution and form of the papillae are quite different in Prochilodontidae. It seems likely that the epibranchial pouches of Curimatidae are of independent origin. In at least one curimatid—"*Pseudocurimata*" *ocellata*—minute conical teeth are evenly distributed in the epithelial lining of the epibranchial pouches. The morphology of both the upper and lower jaws is highly distinctive, as is also the soft anatomy of the mouth and the exceptionally numerous rows of preformed replacement teeth. The interhyal bone is uniquely specialized. Although adequate comparative studies have yet to be made, it seems likely that the viscera (Fig. 29) may offer diagnostic features, for example, the minute and exceedingly numerous pyloric caeca. The intestine is only moderately coiled, in sharp contrast to the exceptionally coiled condition found in Curimatidae at comparable sizes. The

sound-producing mechanism of the males, when it is properly understood and adequate comparative studies have been made, may also prove diagnostic. In my opinion the unique specializations exhibited by these fishes certainly justify their taxonomic rank as a separate family.

RELATIONSHIPS OF PROCHILODONTIDAE

Owing to superficial resemblances in appearance and feeding habits, it has generally been assumed that Prochilodontidae are closely related to Curimatidae, a family in which adults have thin-lipped edentulous jaws. Regan (1911) placed the Prochilodontidae (as the subfamily Prochilodontinae) in his family Anostomidae (consisting also of the subfamilies Anostominae and Curimatinae). Apart from the paired epibranchial pouches, discussed above, there are no shared specializations in support of a close relationship between Prochilodontidae and Curimatidae. The lateral opercular flange characteristic of Curimatidae is absent in Prochilodontidae, and the many striking specializations of the Prochilodontidae are notably absent in Curimatidae (*vide supra*). The evidence favoring relationship between Prochilodontidae and Anostomidae is relatively strong: the extremely specialized conditions in the suspensorium of the jaws characteristic of the two groups, and general similarities in the morphology of the jaws and cranium, including the shape of the ethmoids, frontoparietal fontanel, and presence of only two openings into the posttemporal fossae (versus three openings in Curimatidae).

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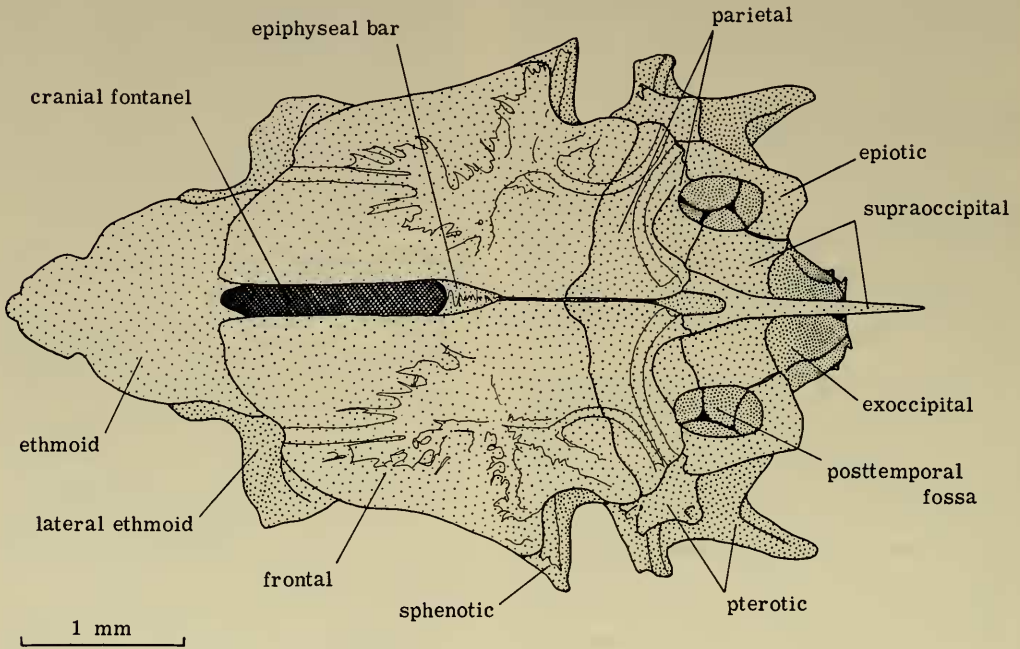
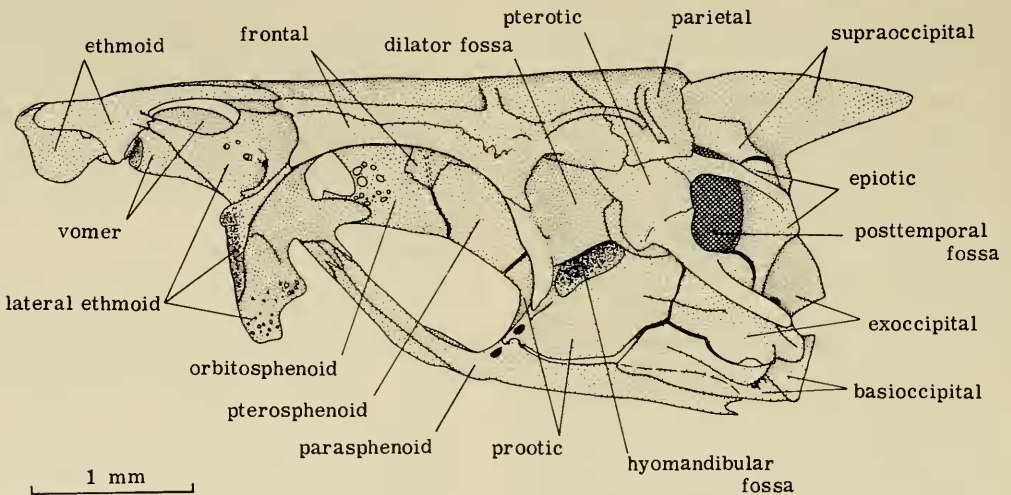Figure 2. *Ichthyoelephas humeralis,* 97.2 mm, dorsal view of cranium.

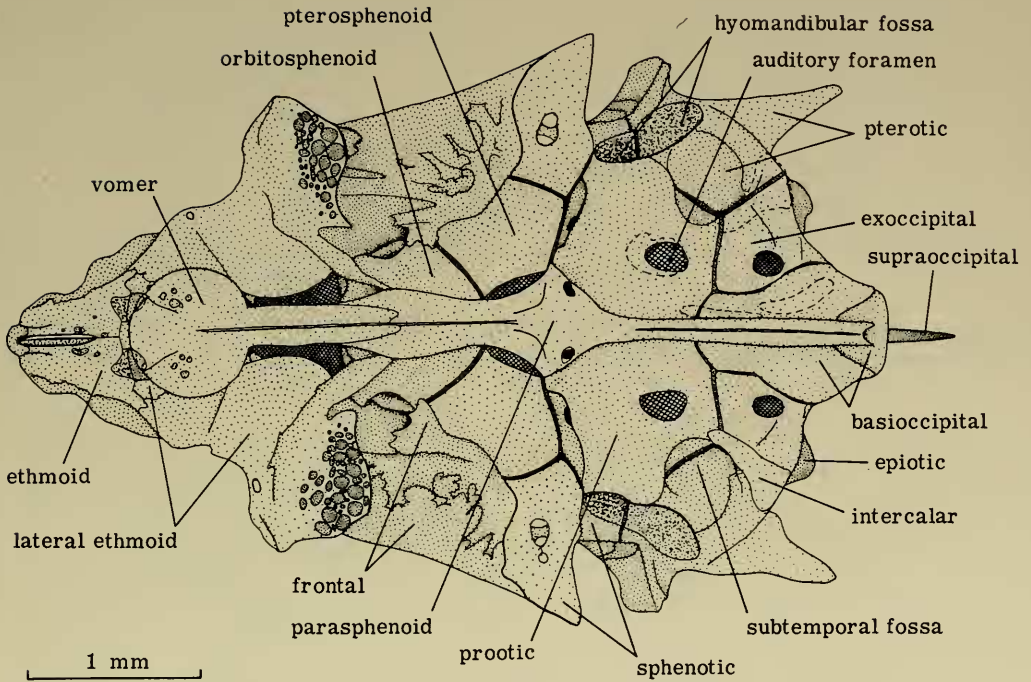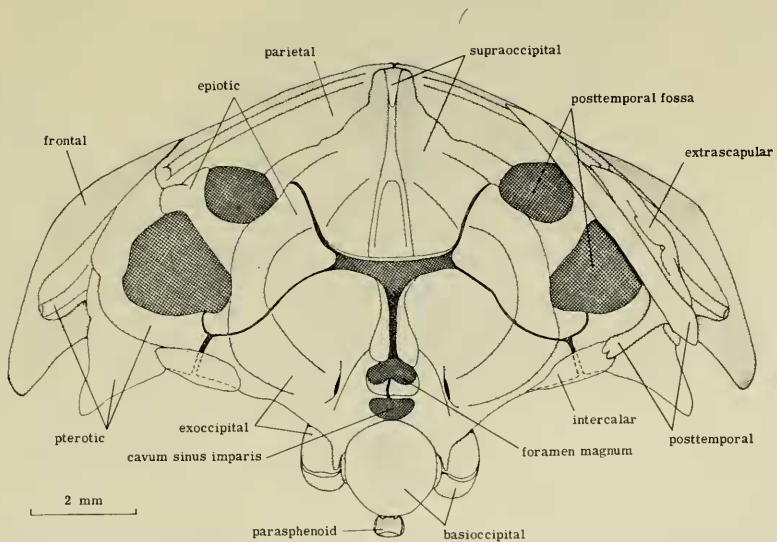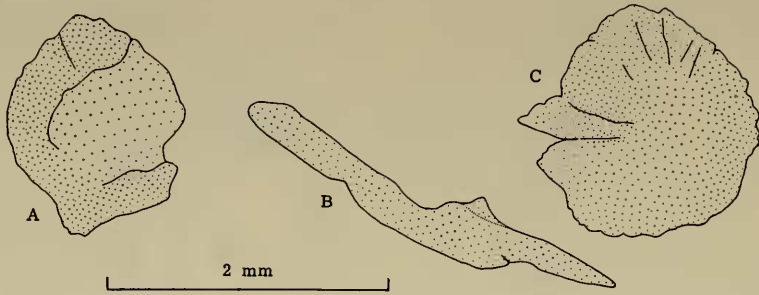Figure 3. *Ichthyoelephas humeralis,* 102.4 mm, lateral view of cranium.

Figure 4.   *Ichthyoelephas humeralis,* 102.4 mm, ventral view of cranium.

Figure 5.   *Ichthyoelephas humeralis,* 102.4 mm, occipital view of cranium.

Figure 6.   *Ichthyoelephas humeralis*, 102.4 mm, otoliths from left side. A. Ventral view of utriculus. B. Lateral view of sagitta. C. Lateral view of asteriscus.
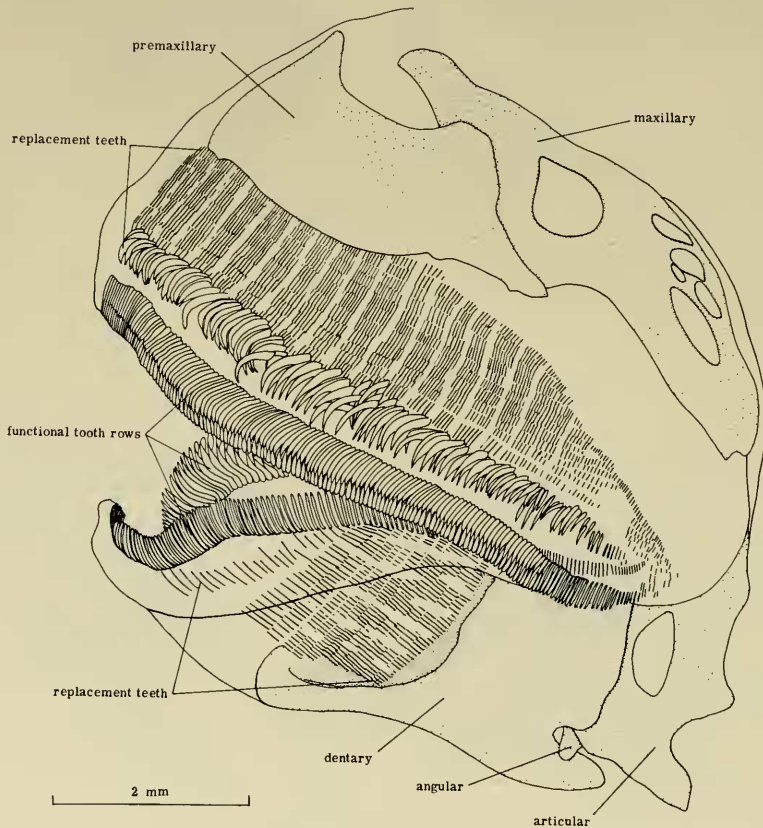
Figure 7.   *Ichthyoelephas humeralis*, 97.2 mm, lateral view of jaws and dentition (internal row of teeth in upper jaw and part of lower jaw hidden from view).
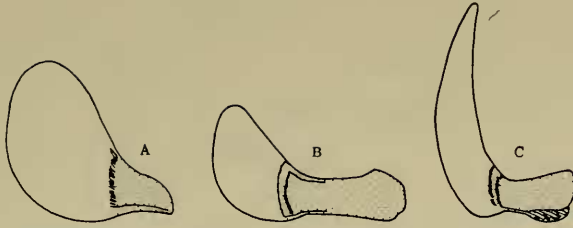
Figure 8. Form of jaw teeth in Prochilodontidae (after Mago Leccia, 1972). A. *Prochilodus.* B. *Semaprochilodus.* C. *Ichthyoelephas.*
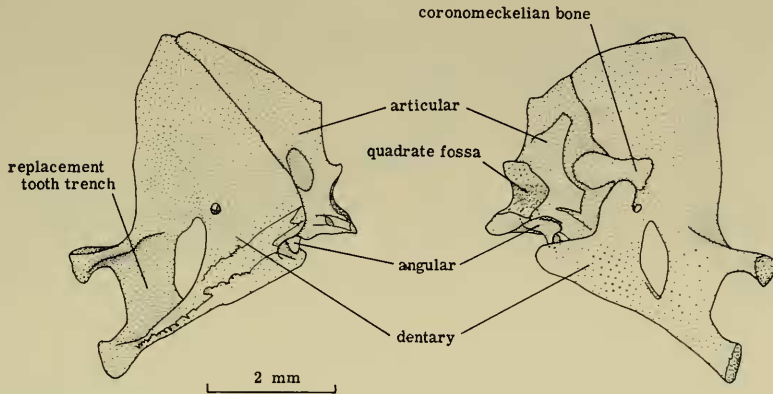
Figure 9. *Ichthyoelephas humeralis,* 97.2 mm, lateral and medial views of lower jaw.
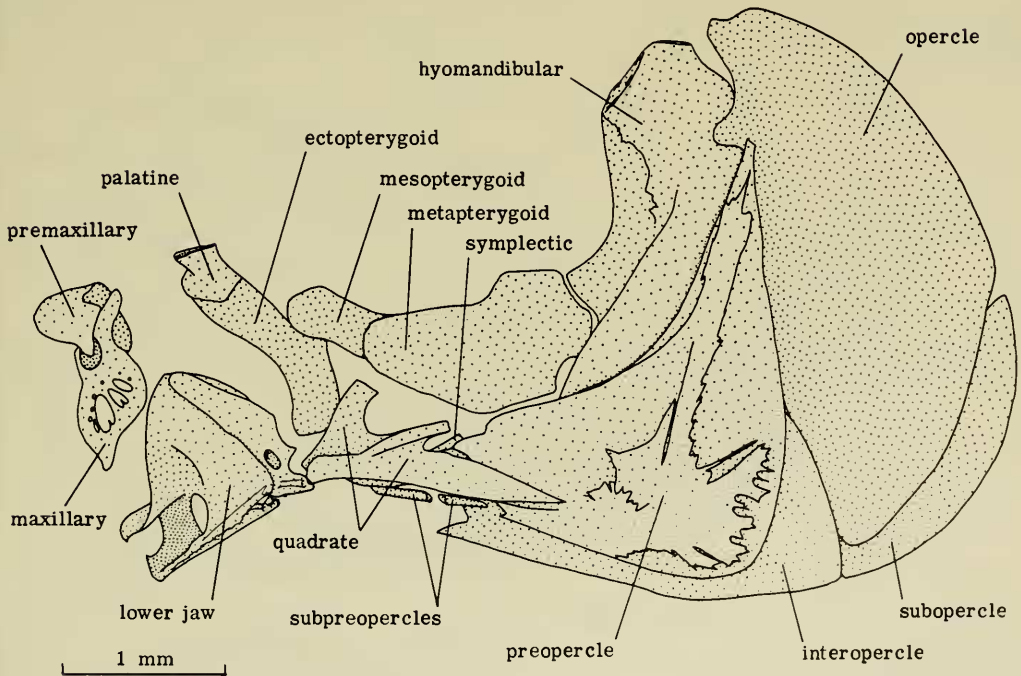
Figure 10. *Ichthyoelephas humeralis,* 97.2 mm, lateral view of jaws, suspensorium, and opercular bones.
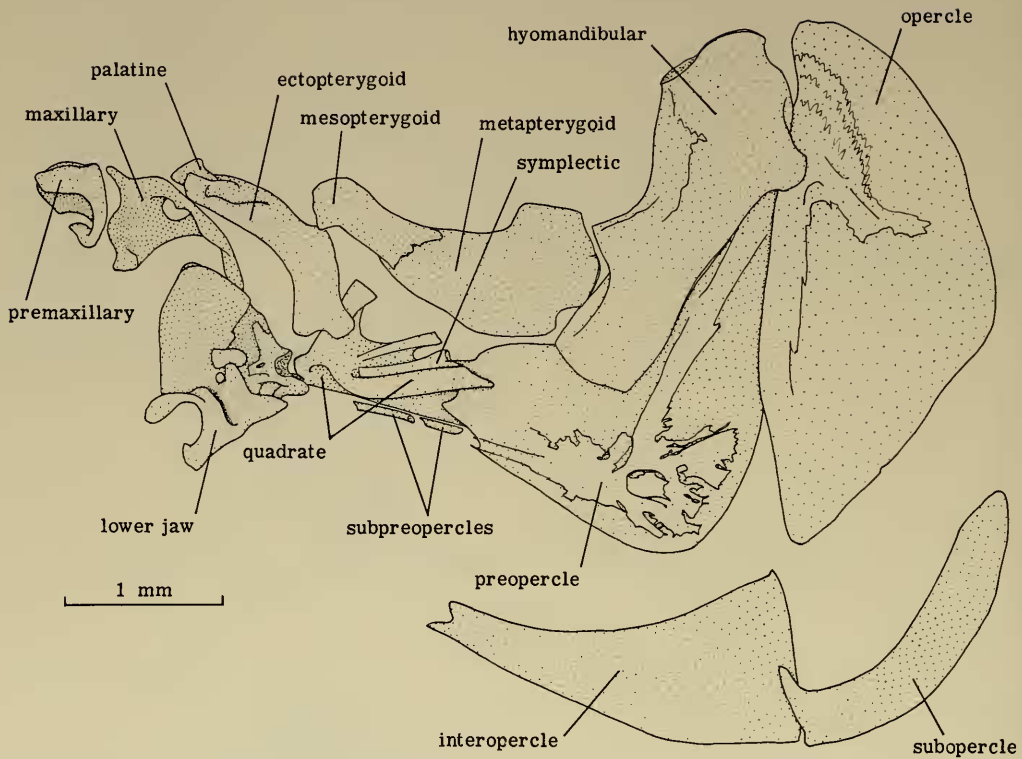
Figure 11.   *Ichthyoelephas humeralis*, 97.2 mm, medial view of jaws, suspensorium, and opercular bones.
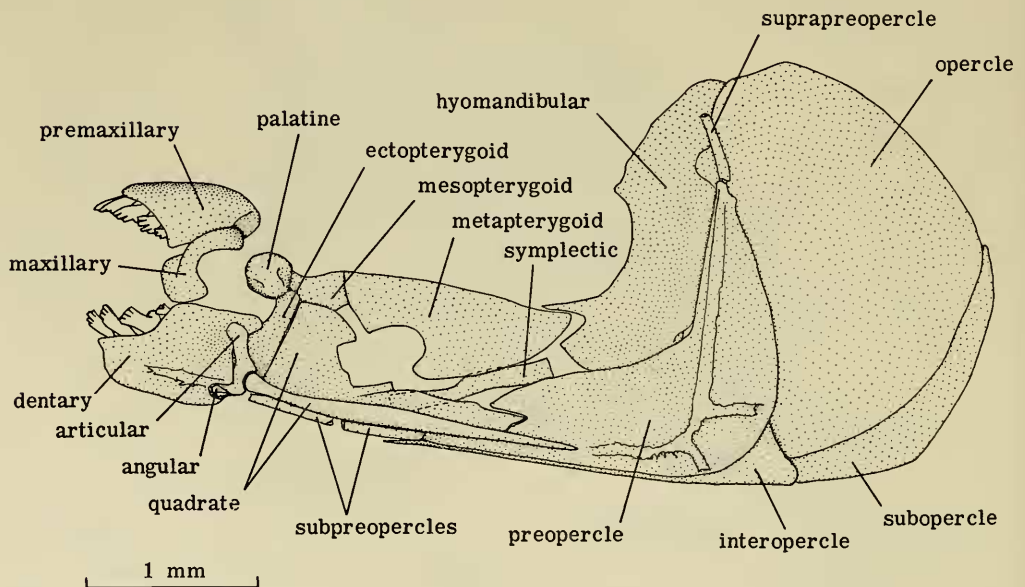
Figure 12.   *Schizodon fasciatus* (Anostomidae), MCZ 46796, 95.3 mm, lateral view of jaws, suspensorium, and opercular bones.
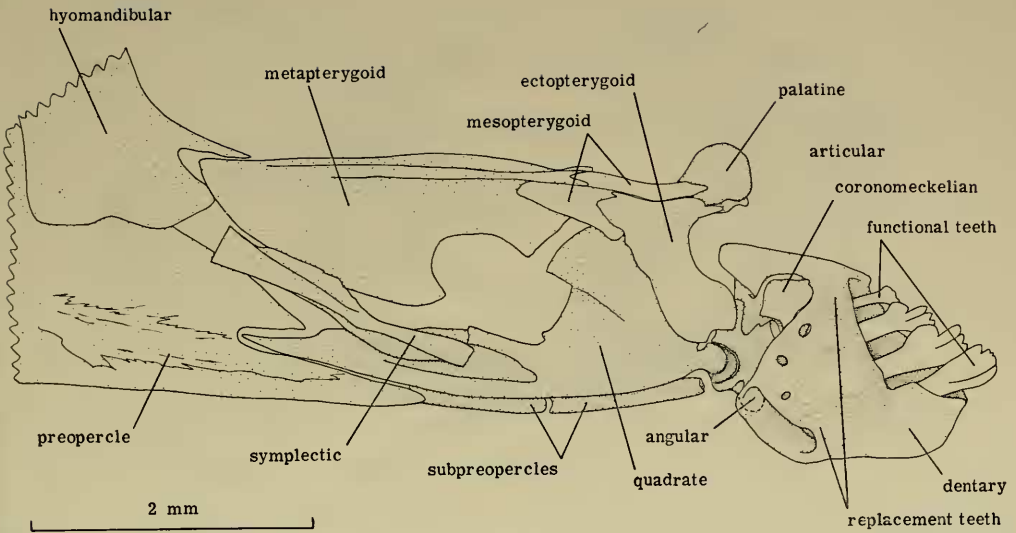
Figure 13. *Schizodon fasciatus* (Anostomidae), MCZ 46796, 95.3 mm, medial view of lower jaw and suspensorium.
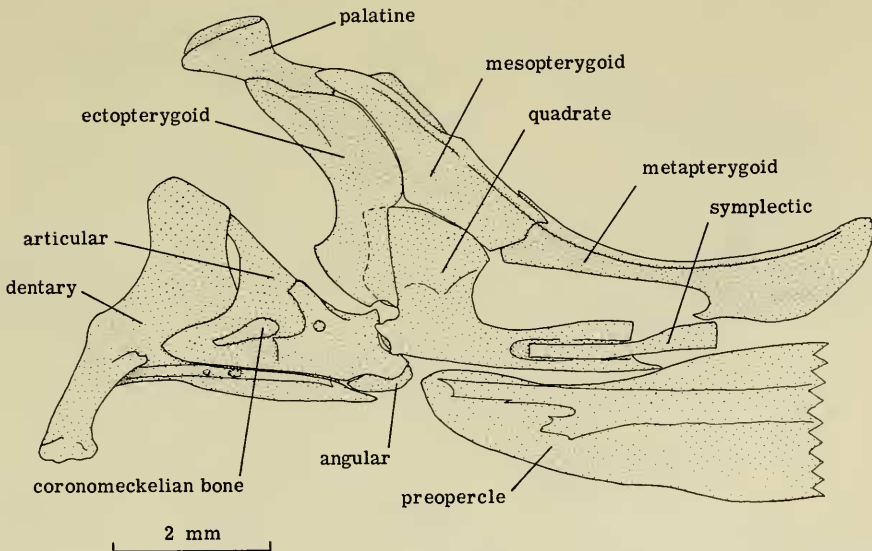
Figure 14. *Acuticurimata macrops* (Curimatidae), MCZ 46801, 69.0 mm, medial view of lower jaw and suspensorium (excluding hyomandibular).
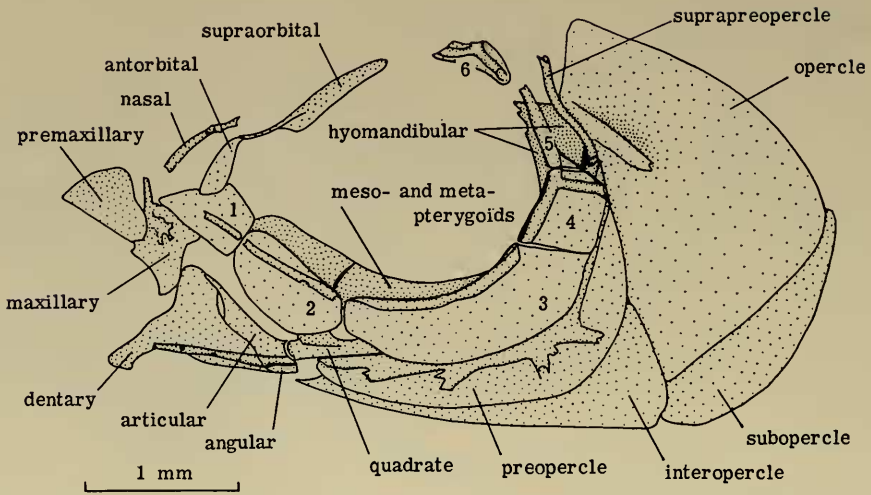
Figure 15. *Acuticurimata macrops* (Curimatidae), MCA 46801, 69.0 mm, lateral view of jaws, facial bones, opercular bones, and suspensorium.
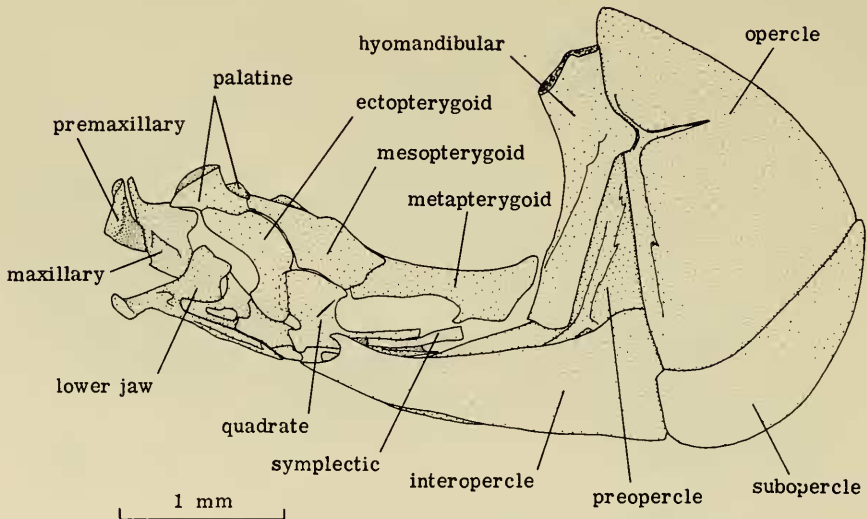
Figure 16. *Acuticurimata macrops* (Curimatidae), MCZ 46801, 69.0 mm, medial view of jaws, suspensorium, and opercular bones.
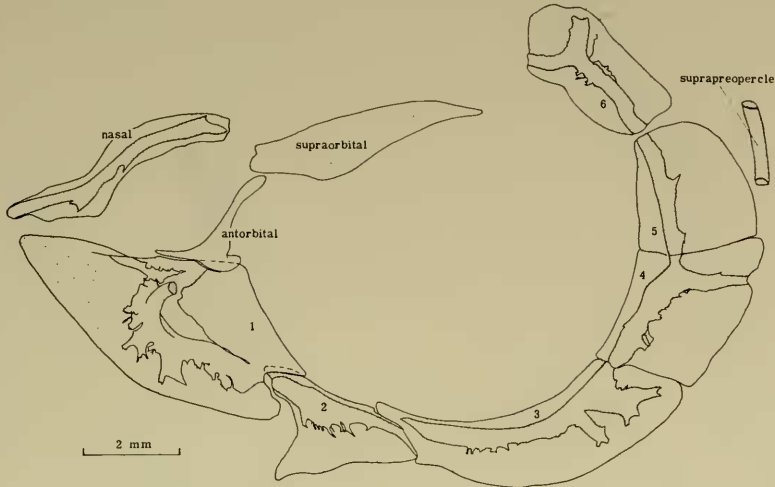
Figure 17. *Ichthyoelephas humeralis*, 97.2 mm, lateral view of nasal, antorbital, circumorbital, and suprapreopercular bones.
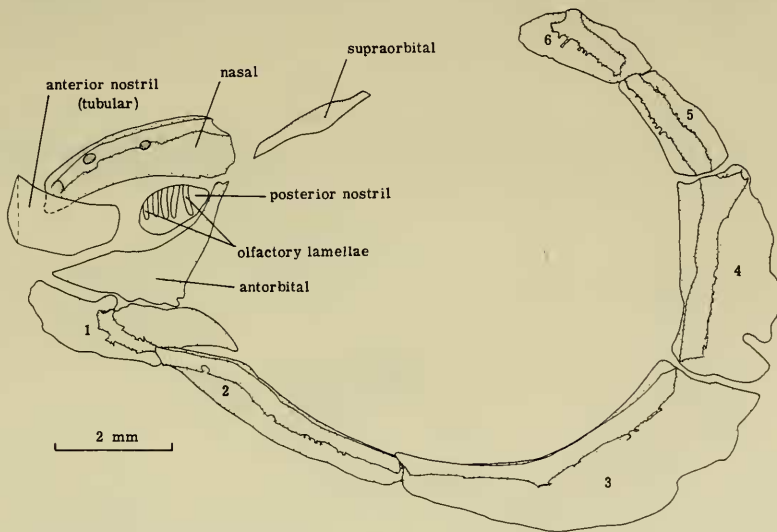
Figure 18. *Schizodon fasciatus* (Anostomidae), MCZ 46796, 95.3 mm, lateral view of nasal, antorbital, and circumorbital bones.
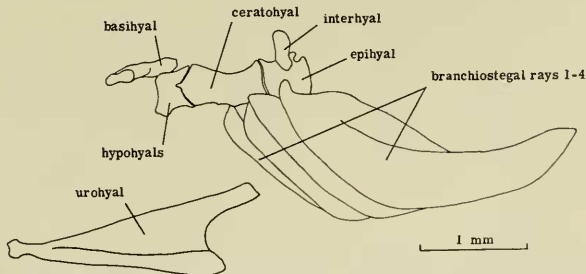
Figure 19. *Ichthyoelephas humeralis*, 102.4 mm, lateral view of urohyal, hyoid bar, and branchiostegal rays.
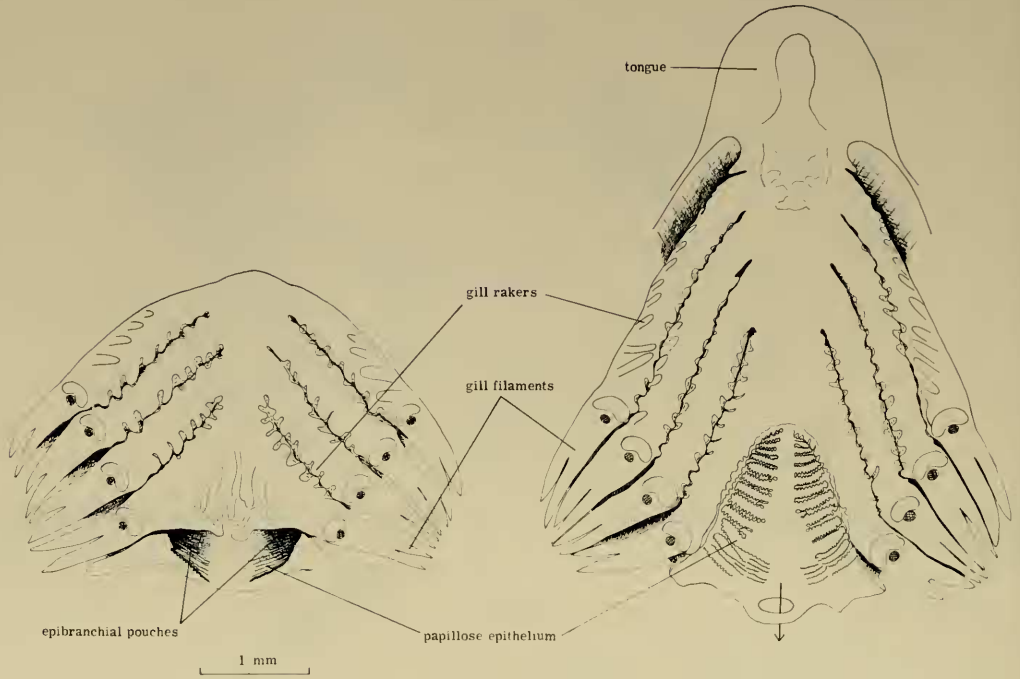
Figure 20.   *Ichthyoelephas humeralis*, MCZ 48805, 137.5 mm, ventral view of upper half of gill structures and dorsal view of lower half of gill structures, showing specialized epithelium and epibranchial pouches.
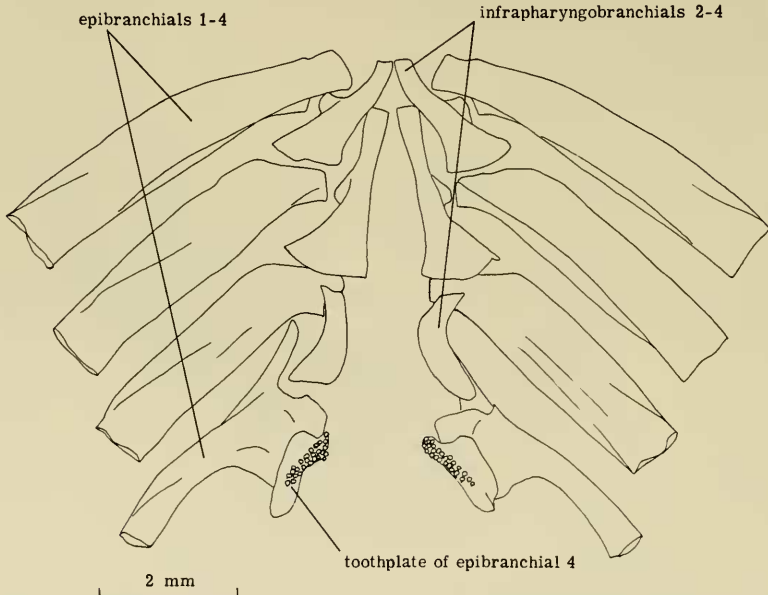
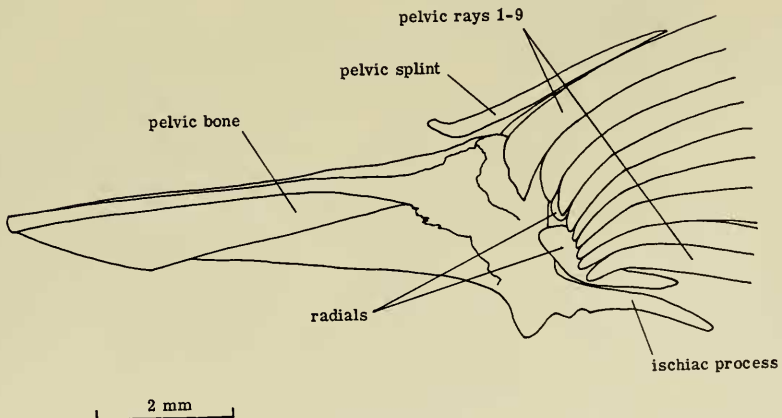Figure 21.   *Ichthyoelephas humeralis*, 102.4 mm, ventral view of dorsal half of gill arches.
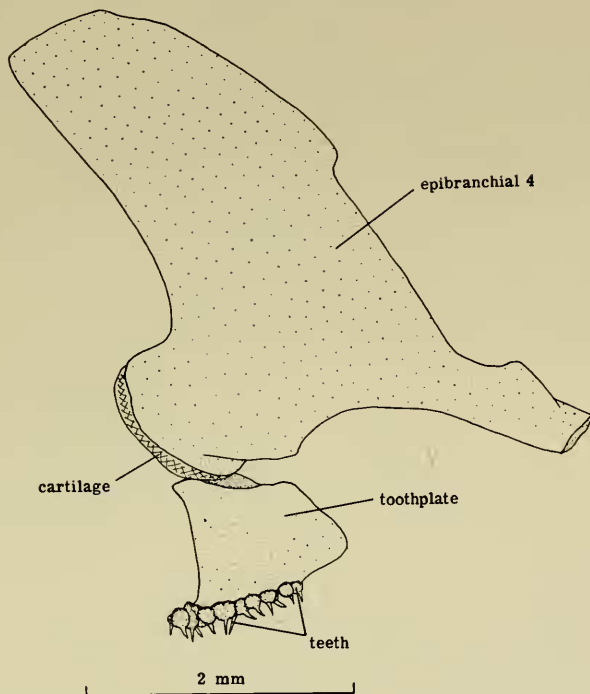
Figure 22. *Ichthyoelephas humeralis,* 102.4 mm, posterior view of epibranchial 4 and its tooth plate from right side of gill arches.
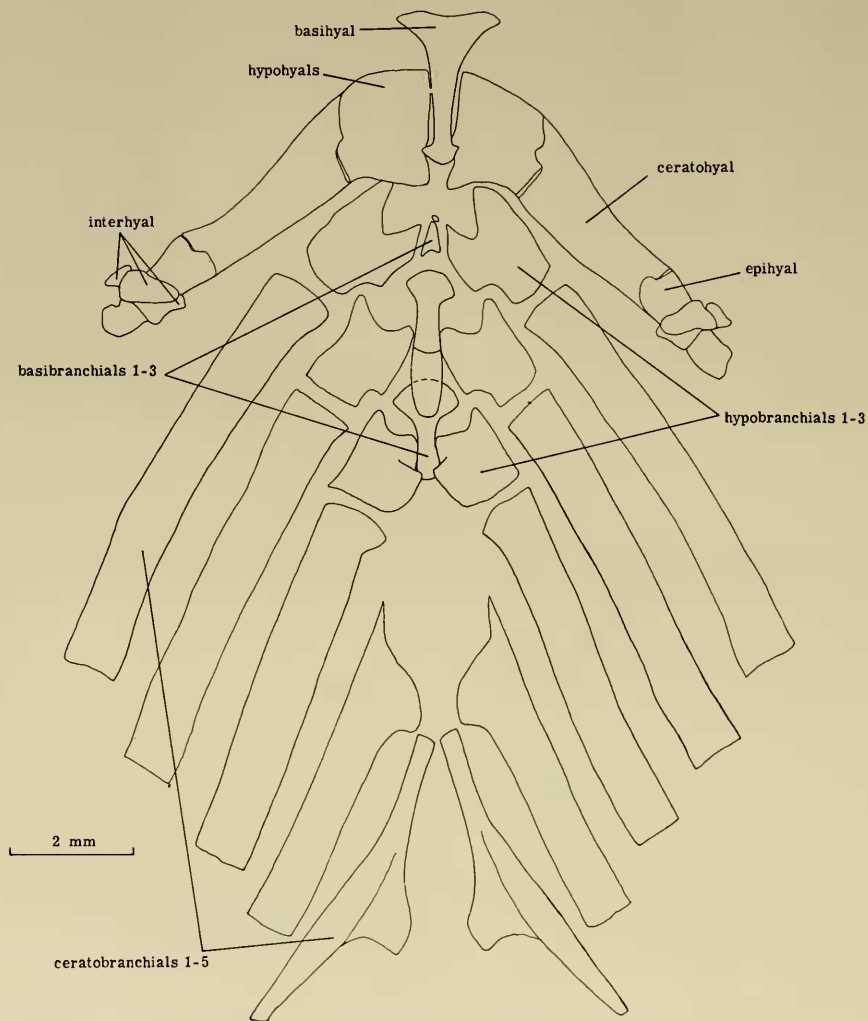
Figure 23. *Ichthyoelephas humeralis*, 102.4 mm, dorsal view of hyoid bar and ventral half of gill arches.
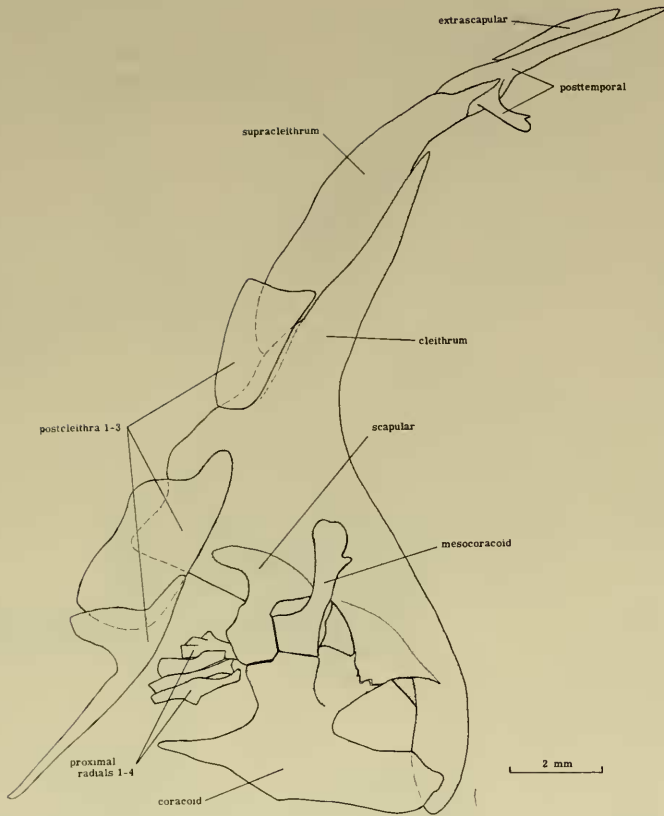
Figure 24. *Ichthyoelephas humeralis*, 102.4 mm, medial view of left half of pectoral girdle.

Figure 25. *Ichthyoelephas humeralis*, 102.4 mm, ventral view of right half of pelvic girdle.
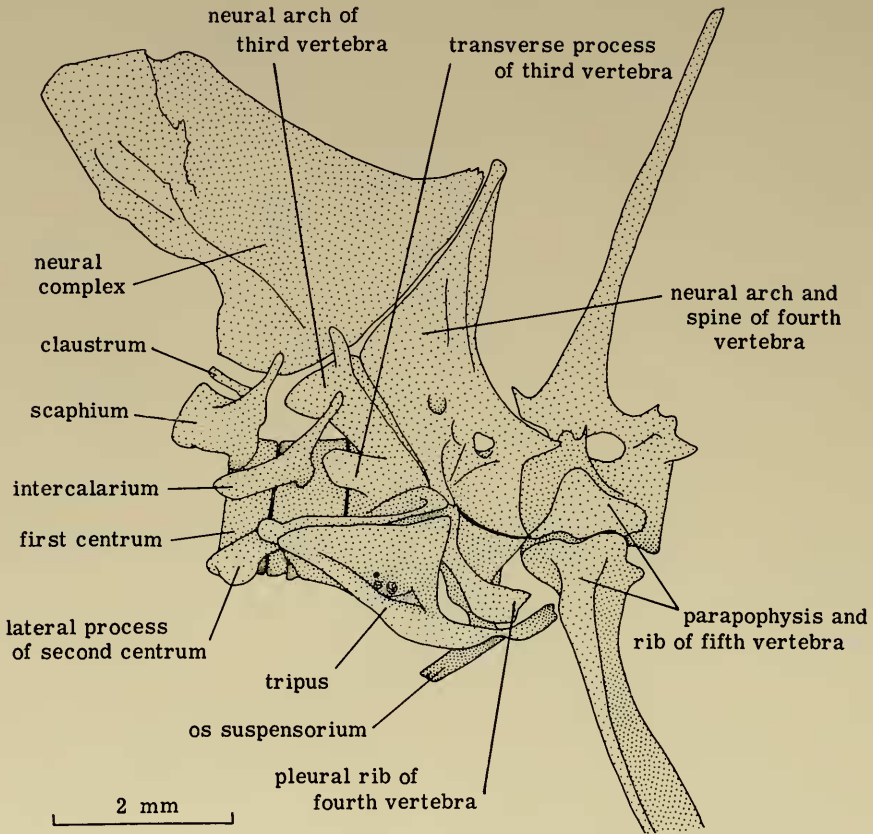
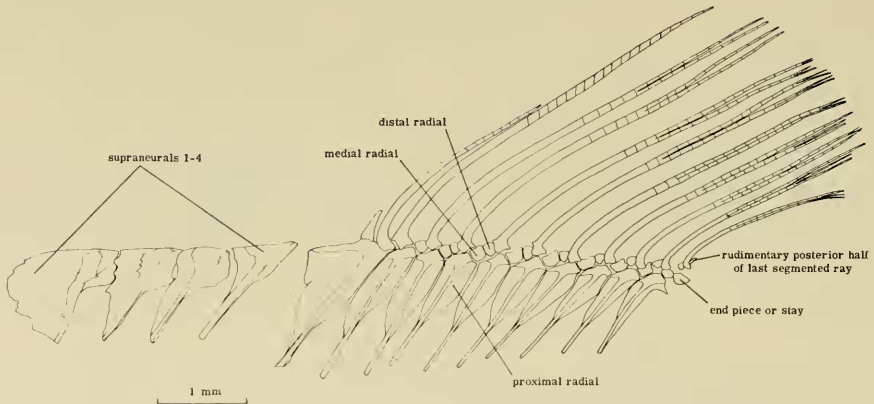Figure 26.   *Ichthyoelephas humeralis,* 102.4 mm, lateral view of Weberian apparatus.

Figure 27.   *Ichthyoelephas humeralis,* 102.4 mm, supraneurals and dorsal fin skeleton.
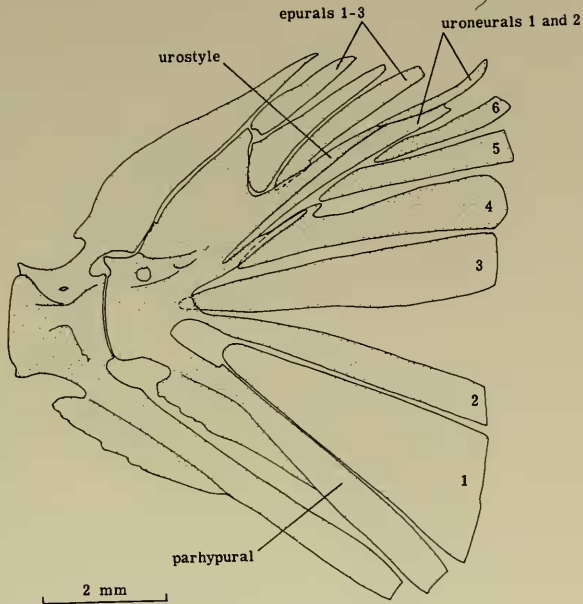
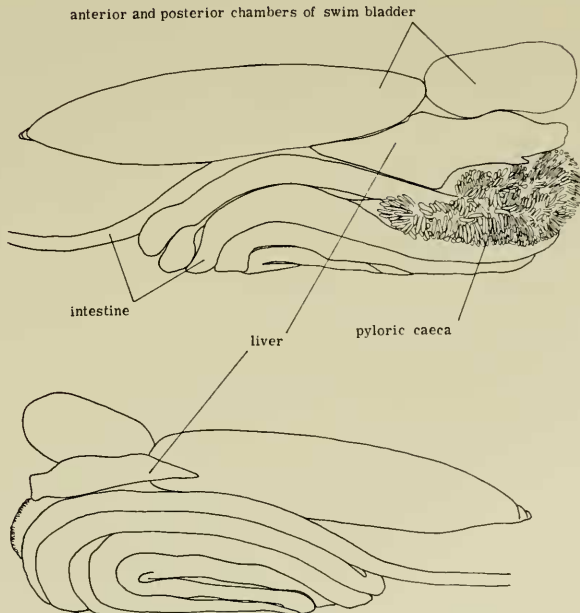Figure 28.   *Ichthyoelephas humeralis*, 102.4 mm, caudal skeleton.

Figure 29.   *Ichthyoelephas humeralis*, 102.4 mm, lateral views of viscera as seen from the right side (above) and from the left side (below).